Grey Heron Ardea cinerea. Up to 7 constantly on shore and reefs or flying over.

Small Green Heron Butorides striatus. 1-2 seen frequently on reefs.

Indian Pond Heron Ardeola grayii. At least 3 present inland.

Honey Buzzard Pernis apivorus. One overhead 13 Feb., identified as a probable bird of the year by the characteristic tail pattern with fine cross bars between the main broad bars.

Domestic Fowl Gallus gallus. Appeared to be established ferally; a brood

of young seen well away from the settlement.

White-breasted Waterhen Amaurornis phoenicurus. One twice seen well inland. Phillips & Sim (1958) noted that some had become entirely terrestrial.

Whimbrel Numenius phaeopus. One on 12 Feb.

Common Sandpiper Actitis hypoleucos. Common all over the island, frequently feeding on sandy tracks inland as well as on the shore.

Indian Cuckoo Cuculus micropterus. One seen frequently.

Koel Eudynamys scolopacea. At least 3 pairs present. House Crows Corvus splendens were exterminated some 10 years previously, so that how the Koels are maintaining themselves is something of a mystery.

European Swallow Hirundo rustica. Small parties seen twice. Common Myna Acridotheres tristis. One seen several times.

In addition, a single tern, probably Sterna sumatrana, was seen twice and on 8 Feb. Mrs. M. S. Fitter briefly saw a bird which could have been a Bronzewing pigeon Chalcophaps indica (blue on head and nape clearly seen), but unfortunately the bird was not seen again.

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## Relationships between hermit hummingbirds and their food plants in eastern Ecuador

by Barbara K. Snow Received 4 March 1981

Hermit hummingbirds, which forage mainly at low levels in forest, provide some striking examples of co-evolution between humming birds and the flowers from which they take nectar. Their feeding ecology has been studied in Trinidad (Snow & Snow 1972, Snow 1973), the Kanaku Mountains of Guyana (Snow 1973), and Costa Rica (Stiles 1975, Snow 1977, Stiles & Wolf 1979). The present paper gives the results of observations made in one of the richest neotropical forest areas, the eastern foothills of the Andes, and discusses the co-evolutionary relationships between this group of hummingbirds and their food-plants.

For 4 weeks, 7 July to 2 August 1976, I was camping with other members of the 1976 Ecuadorean-British Los Tayos Expedition at a height of 600 m in the forested foothills of the Andes in the Morana-Santiago province of Ecuador (3° 06'S, 78° 12'W). The nearest drainage system was that related to the Los Tayos caves into which the streams sank, eventually to join the Rio Coangos which lay c. 240 m below and to the northwest of the camp. The area was covered with primary rain forest except for a felled area in the immediate vicinity of the camp and patches of Indian cultivation, some abandoned. This cultivation was confined to the few more level areas, mostly small in extent, except for a wide strip, about 30 m above the Rio Coangos, which extended for approximately 1200 m. Apart from these flat areas the hillsides are extremely steep and the forests covering them had an abundant herbaceous layer. Within the study area, extending from just below the ridge (c. 900 m) above the Los Tayos stream to the eastern banks of the Rio Coangos, the following 6 hermit hummingbird species were recorded feeding: Threnetes leucurus, Phaethornis superciliosus, P. bourcieri, P. longuemareus, Eutoxeres aquila and E. condamini. Their weights and measurements are shown in Table 1.

TABLE I Weights and measurements of Los Tayos hermit hummingbirds

	wing (mm)	weight (g)	culmen (mm)*
Threnetes leucurus	61 (9)	6.0(2)	34.4(10)
Phaethornis superciliosus	62 (10)	6.5(3)	45.0(10)
Phaethornis bourcieri	56(9)	4.1(8)†	34.7 (9)
Phaethornis longuemareus	35 (2)	3.2(23)‡	25.5 (10)
Eutoxeres aquila	74 (10)	12.2(1)	33.1 (10)
Eutoxeres condamini	72 (9)	13.0(3)	36.1 (7)

Weights were taken in the field at Los Tayos unless stated otherwise. Figures in parentheses are number of specimens.

\*Length of total culmen, not exposed culmen.

†7 weights from Surinam supplied by Dr. F. Haverschmidt. ‡Weight from Snow & Snow 1963.

Hermit hummingbirds usually feed at low levels, mostly on herbaceous plants but also on vines that flower low down and on bromeliads. Therefore to investigate the range of flowers at which these hermits were feeding, watches of half an hour, or multiples thereof, were kept on all plants found flowering below a height of 5 m above the ground and which had tubular corollas coloured yellow, orange or red. Watches were extended to flowers of other colours if any hermit hummingbird was seen feeding at them. Within these criteria probably all the common plants in flower in July were observed in the study area. Observations were not made in cleared ground except on Heliconia aff. wagneriana. The flowers at which the hermits were recorded feeding are listed in Table 2 and their corolla shapes are shown in Figures 1-3. Many of these plants have not yet been identified, but specimens of all of them were collected by the botanists on the expedition and are housed at the Royal Botanic garden, Edinburgh. They are referred to here by the botanists' collection numbers.

In addition to the hermits, 7 species of non-hermit hummingbirds were seen or collected in the Los Tayos locality (Albuja & de Vries 1977). Four of these (Doryfera johannae, Campylopterus villaviscencio, Popelairia popelairii and Taphrospilus hypostictus) were not observed competing or interacting with any

TABLE 2 Food plants floral characters and hermit hummingbird feeding records

		length (mm)	Corolla width (mm)	colour	bract/calyx colour	Height of flower (ft)	Feeding re	cords P.b.	flowers P.L. I	s probed) E.a. E.c.	Total feeding records	Total obs. time (h)
Gesneriaceae.	Drymonia sp. no. 17 no. 237	54 52 41	4 w z.	yellow yellow yellow & red	orange red green	1. 1. 1. 1. 1. 1. 1. 1. 1. 1. 1. 1. 1. 1	8 57 10	*	и и		10 61	1 <del>4 5.</del> 5.
Cucurbitaceae.	Gurania sp.	56	4	orange	green	<u>*</u>	2		*		~	0.5
Rubiaceae.	Palicourea sp.	4	ч	yellow	Breen	OI			6		6	0.5
Lobeliaceae.	Centropogon aff. cornulus	38	9	red	green	2-2 <del>}</del>				53 140	193	4
Musaceae.	Heliconia 35 Heliconia 91 Heliconia vellerigera 23 Heliconia 58 Heliconia 56 (aff. wagneriana) Heliconia 306	3554 g X X	~ 8	yellow yellow yellow yellow yellow yellow	red or yellow red red red red red red pink	TITTTT	2 14 6			62 5 6 6 7	67 2 2 4 4 7	12.5 6 6 1.5 6 12.5
Zingiberaceae.	Costus 102	22	4	yellow	red	402			22		22	3
Bromeliaceae*.	Vriesea aff. rubra Gezmania melinonis Aeslmas strobilicara Pitcairnia aphilandriflora Pitcairnia aff. quamelioides	% 54 54 57 57 57	4 <del>v.</del> <del>1</del> 4 ∞	white yellow red red	pau pau	ııııı	16	9 4	<del>2</del> 4		6 61 12 17	£ 4 4 0 2:1
Marantaceae.	Monotagma aff. plurispicatum	25	1.5	white	green	<u>1</u>	8				7	
Family?	sp. 43 (dicot.)	36	<del>*</del>	orange	red	۴	н					0.5
Total feeding records No. different species	ords ies						16 131	12	87 1	188 149		

TJ = T brenets leavarus. P.s. = P baethorn is supercities as. P.b. = P, bowrier. P.J = P. longumarus. E.a. = E subsects aguila. E.c. = E, condamini.

\*The bromeliads were identified from photographs and sketches. For botanic species' numbers see text.

of the hermit hummingbirds. Thalurania furcata and Chrysuronia oenone were territorial over some plant species (Costus, Palicourea) at which P. longuemareus also fed. Heliothryx aurita was a nectar-thief, piercing the corolla tube and taking nectar from Heliconia 306.

Habitat preferences

There were some recognisable differences in habitat preference between the 6 hermit species. Both T. leucurus and P. longuemareus frequented second growth associated with cultivation as well as forest, and were commoner at the Rio Coagnos level, where there was a lek of P. longuemareus, than elsewhere. P. longuemareus (but not T. leucurus) was occasionally seen feeding along streams, while T. leucurus (but not P. longuemareus) was seen on the forest slopes well above the Los Tayos stream beds. P. superciliosus was the most abundant hermit of the Los Tayos drainage system and commonly fed along its stream banks and also along the Rio Coangos. It was recorded at c. 900 m near the ridge, feeding on the ground bromeliad Pitcairnia aff. quesnelioides. It visited forest edge but not more extensive second growth. P. bourcieri was rather scarce and was not seen below the level of the Los Tayos stream along which it occasionally fed. It also fed up to c. 700 m on 2 bromeliads, Vriesea rubra and Guzmania melinonis. Neither Eutoxeres species was seen feeding above 600 m, but both were found along the Los Tayos stream and Rio Coangos. E. condamini was commoner at dispersed nectar sources, including some in second growth.

Flower preferences

Bill shape and to a lesser extent bill length are the chief characters with which flower preferences of the different hermit species could be matched (Figs. 1-3, Tables 1, 2). The most striking match is between the bills of the sicklebills Eutoxeres and 3 of the Heliconias (35, 23 and 306) and Centropogon cornutus (Fig. 1d). Only the sicklebills fed at these 4 plants except for a nectar thief, Heliothryx aurita, which has a short straight bill and was seen piercing the corollas of Heliconia 306. I spent sufficient time watching these 4 plants (Table 2) to feel confident that no other humming bird was foraging at them; so in this area at least they are probably dependent on the sicklebills for cross-pollination. Both E. aquila and E. condamini perch while feeding at heliconias. Heliconia aff. vellerigera and Heliconia 35 both have pendent, distichous inflorescences (Fig. 1a, b); the bracts which contain the flowers open downwards and the sicklebills perch on the bract below and stretch up with head tilted back to insert their beaks into the corolla above. In Heliconia 306, the bracts do not enclose the corolla—hence its susceptibility to nectar thieves—but a succession of flowers assume an upright position, growing from the axil of the bract and facing outwards (Fig. 1c).

As the Eutoxeres species appear to have exclusive legitimate access to these 4 plant species, territorial behaviour to exclude any other hummingbird except congenerics is superfluous. However in places, Heliconia 35 and Heliconia aff. vellerigera grew in very large clumps and a 4-5 foot band of Centropogon cornutus was flowering along 40 consecutive metres of the Rio Coangos banks; so all these plants were potentially very concentrated sources of nectar. Equivalent nectar concentrations in flowers with less specialized corolla shapes would, on the other hand, be defended as feeding territories (Stiles 1975, Lyon 1976), with much inter- and intra-specific competition. E. aquila and E. condamini are not very different in size; condamini has a



Fig. 1. Flowers at which Eutoxeres aquila was observed feeding; (b) and (d) were also fed at by E. condamini. (a) Heliconia 23, aff. vellerigera. (b) Heliconia 35. (c) Heliconia 306. (All Heliconia showing corolla without bract, part of inflorescence and position of Eutoxeres when feeding. (d) Centropogon cornutus calyx emoved.

single corolla.(e) Drymonia sp. (P.s. and P.I.). Flower with leaf-like bract and single corolla. (f) Aechmea strobilacea (P.s. and P.I.), corolla surrounded by protective These 2 bromeliads show the corollas embedded P.s.), corolla with calyx removed. (d) Piteairnia quesneloides (P.s.) inflorescence and and Phaethornis longuemareus (P.1.) were observed feeding. (a) Guzmania melnonii in their protective bracts and corollas without bracts.)(c) Gesneriaceae 17(P.b. and Fig. 2. Flowers at which Phaethornis bourcieri (P.b.), Phaethornis superciliosus (P.s. bracts, and with bracts removed. (g) Pittairnia aphelandriflora. P.b.). (b) Vriesea aff rubra (P.b.).

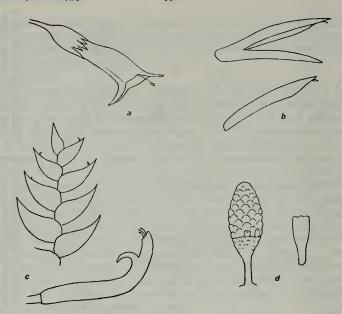


Fig. 3. Hummingbird abbreviations as in Fig. 2. (a) Gesneriaceae 237 (P.s. and P.l.), (b) Heliconia 57 (P.s.), corolla and enclosing bract and (below) with free part of bract removed. (c) Heliconia 56 (P.s., T. leucurus & E. condamini), inflorescence and corolla without bract. (d) Costus sp. (P.l. & non-hermits), inflorescence cone and corolla removed from cone.

slightly shorter wing but a longer bill (Table 1), so some behavioural differences between them might be expected for co-existence. In fact E. aquila showed some territorial behaviour and was seen driving off E. condamini and conspecifics. Only E. aquila was seen feeding at the 2 shaft entrances of the Los Tayos caves, which provided permanent light gaps enabling large stands of Heliconia 35 and Heliconia aff. vellerigera to grow there. Here also, in the early mornings, it uttered advertising songs from solitary perches. On the other hand, no advertising song or territorial behaviour was heard or seen from E. condamini and its foraging suggested interstitial traplining (sensu Colwell 1973). Thus it fed at Heliconia 56 at which E. aquila was not seen to forage. T. leucurus and P. superciliosus also fed at Heliconia 56, hovering at the higher flowers free of entangling vegetation; whereas E. condamini perched to feed often at the lower flowers closely entangled in undergrowth. The two patches of Heliconia 35 at which E. condamini was seen to forage were small ones, also in dense second growth. E. condamini foraged at the large stretches of Centropogon cornutus, but was here occasionally driven off by E. aquila. When feeding at C. cornutus, E. aquila fed perched with folded wings, whereas E. condamini only did so at about a third of the flowers it visited, at the other two thirds clinging on, but continuing to beat its wings while feeding.

The straight bill of *P. bourcieri* closely matches the corollas of the 3 flower species at which it foraged. It shared one, Gesneriaceae 17, with *P. superciliosus*, but it is very unlikely that any other hermits beside *P. bourcieri* fed at the 2 bromeliads at which it foraged. A very narrow constriction of the

corolla (to about 1 mm diameter) in both the bromeliads, at the aperture in *Vriesea rubra* and in the middle of the corolla tube in *Guzmania* aff. *melinonis* (Fig. 2b, a), would make entry by a hermit with a curved bill virtually impossible.

TABLE 3
Percentage feeding at flowers of different corolla lengths by 3 hermit hummingbirds.

		Corona	rengths (in	.11)	Total
	20-29	30-39	40-49	50-59	records
P. superciliosus	2	8	25	65	137
P. bourcieri		67		33	I 2
P. longuemareus	39		56	2	87

P. superciliosus was seen foraging at 11 different flower species, with corolla shapes varying from almost straight to moderately curved. Over half of these were also visited by ot herspecies of hermit, mostly by P. longuemareus. P. superciliosus differed from the latter mainly by its preference for flowers with longer corolla tubes (Table 3). The only flower species in full bloom for which P. superciliosus appeared to be the exclusive pollinator was the bromeliad Pitcairnia aff. quesnelioides with a very long corolla. There was fairly conclusive evidence that it avoided the small-flowered Costus whose inflorescence cone grows at ground level, as one Costus and a ground-living bromeliad, Aechmea aff. strobilacea, were growing close together and could be watched simultaneously. While P. longuemareus visited both plants, P. superciliosus came regularly to the bromeliad but ignored the Costus.

Three of the plant species at which P. longuemareus foraged, Palicourea sp., Gurania sp. and Costus, were also exploited by small non-hermit humming-birds (Thalurania furcata and Chrysuronia oenone). The effective corolla lengths (sensu Stiles 1975) of these 3 plants were between 22 and 26 mm, compared to 41-54 mm for the 4 species at which both P. longuemareus and P. superciliosus

foraged.

## Discussion

In spite of the incompleteness of the data, some comparisons with the feeding of hermits elsewhere are worth drawing. A study by Stiles (1975) of the nectar foraging of 4 hermits (P. superciliosus, E. aquila, Threnetes ruckeri and Glaucis hirsuta) on 9 Heliconia species in the Caribbean Lowland tropics of Costa Rica showed P. superciliosus to be the most abundant hermit, foraging at all the heliconias, whereas E. aquila fed at only one species, H. pogonantha, which has the most curved corolla. However, all the other hermits and 5 non-hermits also fed at H. pogonantha, so E. aquila did not have exclusive nectar foraging at any heliconia as the two Eutoxeres species appeared to have at Los Tayos.

Possibly the very high rainfall areas of the eastern slopes of the Andes are the centre of evolution of *Eutoxeres*, where co-evolution with heliconias is most advanced. *E. condamini* is confined to this region, but *E. aquila* occurs also on the Pacific slopes of Colombia and Ecuador, and extends north to Costa Rica. Possibly *E. aquila* is derived from a population that was isolated in one of the northwestern forest refuges during the Pleistocene (Haffer 1974) and subsequently spread south to overlap with *E. condamini*. That it may still be spreading south is suggested by a single specimen recently collected in northeast Peru (Zimmer 1950), while *E. condamini* ranges to southeast

It is interesting that in Costa Rica the 2 main nectar sources for E. aquila

are the pogonantha group of Heliconias (Stiles 1979a) and Centropogon species (Stiles, pers. comm.), so near the extremes of the range of E. aquila it appears largely to depend on the same plant genera. Heliconia aff. vellerigera and Heliconia 35 have many characters in common with the pogonantha group, e.g. very large pendent distichous inflorescences which showed much

evidence of being long-lived.

In the tropical forest of the Kanaku mountains of southern Guyana (Snow 1973), P. superciliosus was the most abundant of the 4 resident species of hermits, the others being G. hirsuta, T. leucurus and Phaethornis ruber. Thus in 3 well separated areas in Costa Rica, Guyana and Ecuador P. superciliosus is the most abundant hermit hummingbird, although the plant species on which it feeds differ in each locality, with the possible exception of one Heliconia. In Guyana, as at Los Tayos, T. leucurus was rather sparse. The closely related T. ruckeri is also relatively sparse in the area of Costa Rica in which it was studied (Stiles 1975). Whatever the factors are which control relative abundance in P. superciliosus and species of Threnetes, they appear to operate over a wide geographical range and in forest habitats supporting almost entirely different plant species.

Six plant groups (families or genera) together provide a high proportion of the nectar taken by hermit hummingbirds in the 3 places in South America where observations have been made (Table 4). Climatically the Kanaku mountains of Guyana differ from the 2 other areas in having a fairly severe dry season (during which most of the observations were made). Bromeliads were absent and the Passifloraceae, not recorded at the other 2 wetter areas, were important.

TABLE 4

Percentage use of 6 plant families/genera by hermit hummingbirds for nectar feeding.							
	Acanthaceae	Bromeliaceae	Heliconia	Costus	Centropogon	Palicourea	
Trinidad (782)	18	9	36	9	7	8	
Los Tayos		17	29	4	33	2	
Guyana	31		4	22			

Figures in parentheses below localities are total feeding records. In Los Tayos one flower probed was one record. In Trinidad and Guyana a record constituted a bout of feeding at a plant species.

At Los Tayos, as elsewhere, many of the hermit-exploited flowers have evolved means of protecting their nectar from illegitimate exploitation by nectar thieves who do not perform pollination. Thus of the six *Heliconia* species at which hermits were feeding three, *Heliconia* aff. vellerigen, 35 and 56, have approximately two-thirds of their corollas embedded in a thick, often hairy bract (Figs. 1, 3). *Heliconia* 57 has the corolla and thickened calyx entirely fused (Fig. 3b). The flowers of 2 species are unprotected; one of these, *Heliconia* 306, was seen to have the corolla pierced; no hummingbirds were seen taking nectar from the other, *Heliconia* 58.

Three of the 5 bromeliads (*Vriesea rubra*, Aechmea aff. strobilacea and Guzmania aff. melinonis) have approximately two-thirds or more of the corolla protected inside thick-walled bracts, with the flowers concentrated into compound inflorescences: Guzmania sp. as a red elongated cone, Aechmea sp. as a large round bristling cone at ground level, and *Vriesea rubra* as a flattened branching inflorescence (Fig. 2). The flowers of the two *Pitcairnia* 

species are less well protected and many of the corollas of Pitcairnia aphelandriflora were found to be pierced just above the calyx (Fig. 2). The Costus species also has the base of its corolla embedded in a protective cone

(Fig. 3).

As an hypothesis, I suggest that plant genera that have co-evolved with hermit hummingbirds in the direction of increased corolla length or specialized corolla shapes, to match the hermit's increased beak length or curvature, and which also offer a fairly substantial nectar reward to make a visit to these often scattered plants worthwhile—that these plant genera have had to evolve protection for their nectar from short-billed hummingbirds that acquire flower-piercing habits (e.g. Heliothryx aurita) and from the flowerpiercers Diglossa spp. Stiles (1979a) has already suggested this as an adaptation of heliconias that may deter nectar thieves.

Only 2 of the bromeliads utilized by hermits at Los Tayos are epiphytic on trees: Vriesea rubra which grew at heights of 1-1.5 m, often on understorey trees, and Guzmania sp. which grew at heights of 1.5-10 m. Such low-growing habits are probably also an adaptation for pollination by

low-flying hermit hummingbirds.

Gesneriaceae 237, an herbaceous plant 0.5-0.7 m high, presents its yellow flowers so that they are visible only to low-flying hummingbirds. It has a horizontal spread of leaves whose upper surface is green and under surface is red; the yellow flowers grow just below the red under surface of the leaves and are not visible from above. The use of red pigment in otherwise unmodified leaves as part of the attraction unit (sensa Stiles 1980) in ornithophilous flowers has been reported in other Gesneriaceae species (Jones & Rich 1972).

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## Present abundance of the Warsangli Linnet Acanthis johannis

by J. S. Ash and J. E. Miskell
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It seems likely that the present-day status of the elusive Warsangli Linnet Acanthis johannis has changed considerably from what it was in the recent past. In May 1979 we found it was one of the commonest small birds round Daloh (10° 45'N, 47° 15'E) in the mountains of northern Somalia, that is in one of the 2 earlier collecting sites; and in May 1980 we saw others at 2 new sites, namely Moon (11° 01'N, 48° 26'E) and Ragad (10° 59'N, 48° 31'E), close to the second earlier collecting site near Musha Aled (11° 00'N, 48° 19'E).

Archer & Godman (1961) reviewed the existing paucity of knowledge about the species (see also Clark 1919, Williams 1956), whose past occurrences and distribution can be summarised as follows:- "On the way up to Musha Aled" 1200 m, 8-9.ii.1919, flock of 25 seen, 1 & collected on 9.ii.1919; Daloh 1800 m, 12-13.viii.1955, small flock, 1 & collected 13.viii and 1 & collected 22.x.55; [Bokh (10° 36'N, 47° 12'E) 1800 m, 1955, stated to occur]; and Tagair (10° 45'N, 47° 24'E) 1760 m, 27.vii.1957, 1 & collected (USNM

487690).

A. R. Tribe who lived at Daloh for some time, and collected all the later specimens, saw more of these linnets in the area on other occasions at 1800-2100 m, and the specimen collected by him at Tagair suggests that there may be still other specimens unrecorded in the literature. Archer's collector was unable to find the birds in nearly 2 months search from March 1919, and neither R. Meinertzhagen in about 1950 nor J. G. Williams in 1954 could find it in the Warsangli country. We intended to look for the species on our journey in May 1979 from Erigavo (10° 38'N, 47° 22'E) to Mait (10° 58'N, 47° 05'E) through Daloh, but hardly expected to find it in the short time at our disposal, particularly in view of the infrequency of sightings in the 60 years since its discovery.

As we approached the Rest House in the Daloh Forest Reserve on 17 May we stopped to watch, as it flew up into a tree, the first Somali Blackbird Turdus olivaceus ludoviciae we had seen. Close beside it was a Warsangli Linnet. Within the next hour or two we saw many more of the former, and at least 15 of the linnets within 2 km of the Rest House. On the following morning we caught 19 linnets, all males, in 2 nets by small pools, and noted that the birds were very common. On 19 May at a brief halt in a gorge c.5 km to the WNW we saw 10 more males, but failed to see any others on the steep descent to the coastal plain. The wing-lengths of the captured birds ranged from 70-80 mm, mean 75.2 (S.D. ±2.80) and the weights from 11.8-15.0 g, mean 13.4 (S.D. ±0.78).

Daloh is situated in degraded Juniper Juniperus procera forest, with some olives and other mixed trees and shrubs, where there were many open areas